Chapter 5

Soil Algae

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I. ABUNDANCE IN AND ON SOIL

Algae are found in soils everywhere (for recent reviews see Lund, 1962, Shields and Durrell, 1964). Satisfactory methods for estimating rates of production (productivity) have not been devised. Populations (production) are estimated by three main methods (Bristol Roach, 1927a; Petersen, 1935; Lund, 1945–46; Brendemühl, 1949; Tchan, 1952, 1953, 1959; Tchan and Bunt, 1954; Shtina, 1956b; Vaidya, 1964). First, by direct observation, sometimes with the aid of fluorescence microscopy. Second, by dilution cultures. A known amount of soil is placed in a liquid or on solid medium, usually agar; by repetition of this process smaller and smaller amounts of soil can be sampled and the number of algae appearing in each dilution later estimated. Third, by extracting the chlorophyll with acetone or methanol and measuring it spectrophotometrically. The variability of the estimates of maximum numbers or biomass of algae in Table I may be related partly to the different methods of estimation and partly to seasonal variations in abundance. Though the estimation of biomass may be a "very superficial calculation" (Potul'nitskiĭ, 1962) Russian work suggests that the amount of organic matter produced by algae can be very considerable and that their importance in soil processes has been underestimated (Table II); see also Shtina, 1964a, b.

Algae are usually most abundant at or close to the surface but may also be

found in the lower horizons of the soil (Fig. 1). Sometimes the largest population is found a few centimetres below the surface (Bristol Roach, 1927a; John, 1942; Flint, 1958) where there will be insufficient light for photosynthesis (Sauberer and Härtl, 1959; Durrell and Shields, 1961). It may be,

TABLE I

Maximum number of algal cells found in diverse types of soil from various parts of the world

Cells/g × 10⁻³	Depth in cm	Notes	Type of land or soil	Country	Reference
800	0–0·4	B.D.*	virgin, sandy	Australia	Tchan (1953)
462	0	B.D.	garden	Denmark	Petersen (1935)
3,000	0	B.D.	garden	Denmark	Petersen (1935)
40	0	B.D.	pasture	Denmark	Petersen (1935)
10	0	B.D.	arable	Denmark	Petersen (1935)
20	0	B.D.	acid heath	Denmark	Petersen (1935)
10	0	B.D.	forest	Denmark	Petersen (1935)
149	0	B.D.	grazing	Denmark	Petersen (1935)
106	0–2·5	B.C.	manured	England	Bristol Roach (1927a)
130	0–2·5	B.C.	manured	England	Bristol Roach (1927a)
37	0–2·5	B.C.	unmanured	England	Bristol Roach (1927a)
333	0	B.D.	virgin, bird dung	Greenland	Petersen (1935)
793	?	?	forest	Hungary	Féher (1933)
510	3	B.C.	cultivated	Italy	Florenzano et al. (1963)
548	0	A.C.	limed	U.S.A.	Stokes (1940)
800	?0–5	?B.C.	arid	U.S.A.	Martin (1940)
329	?0–5	B.D.	virgin, ploughed	U.S.S.R.	Shtina (1954)
229	?	B.D.	fertilized	U.S.S.R.	Shtina (1954)
188	0–5	B.D.	grassland	U.S.S.R.	Shtina (1954)
28	?	B.D.	virgin, tundra	U.S.S.R.	Shtina (1964)
94	?	B.D.	solod	U.S.S.R.	Shtina (1959)
155	0–10	B.D.	fallow sod-podsol	U.S.S.R.	Shtina (1957)

* A, air-dried soil; B, soil not dried; C, estimation by dilution cultures; D, by direct observation. In the Danish and Greenland soils the number of cells per cm^3 is given.

therefore, that these aggregations are produced by the action of rain on superficial growths, but there is still some uncertainty about the amount of growth possible in the dark under natural conditions. Féher (1948) found nearly 700 species at 15 to 20 cms below the surface of soils from many parts of the world. He says that this is the depth "where can be found the highest intensity of soil life." However, many of the algae are aquatic and, without confirmation, his data are open to considerable doubt. Rain and earthworms are believed to be the chief agents in the vertical transport of algae (Petersen, 1935; Tchan and Whitehouse, 1953). Many soil algae are able to return to the surface if they are not buried too deeply. Nearly all the

diatoms and Cyanophyta are motile forms, and many Chlorophyta and Xanthophyta produce zoospores, especially when they are wetted after a dry period. Among pigmented flagellates, the commonest are species of *Chlamydomonas* and *Euglena*. Though motility may be of biological advantage over small distances and in relation to the microclimate, distribution over greater distances seems to be in wind-borne dust (Bock, 1963; Brown, Larson and Bold, 1964; Schlichting, 1964).

TABLE II

Abundance of algae in certain virgin soils and in four cultivated chernozems of the U.S.S.R.

Virgin soils*	Cells/g $\times 10^{-3}$	Biomass (kg/ha)
Sod podsol	10–208	40–300
Podsol	5– 30	7– 20
Boggy podsol	6– 50	10– 45
Peaty-boggy	5– 80	20– 80
Alluvial meadow	52–300	80–450
West-Siberian chernozem	48	16
Dark chestnut	2,150	187
Solonetz-meadow, deep columnar	988	515
Solonetz-steppe, deep columnar	392	74
Solonetz-crusty, nutty	5,146	429
Cultivated chernozem		
Under red oats	755–2,161	194–494
gooseberries	588–1,702	134–436
strawberries	181–1,578	55–525
Vegetable garden	390–2,043	98–546

* In the virgin soils average abundance from the surface to 10 cm depth, except for the chestnut and solonetz soils where the depth range is 0–2 cm. In the cultivated chernozems under different crops the Cyanophyta and Chlorophyta were counted together and all the figures shown were obtained from samples 5 cm below the surface.

Data from Shtina, 1959a and Potul'nitskiï, 1962; for later data on number of cells present see Shtina, 1960, 1964a.

Such evidence as is available about their periodicity shows that the same species may be found throughout the year and from one year to another (Lund, 1945–46, 1947; Shtina, 1959b; Forest, Willson and England, 1959; Potul'nitskiï, 1962). In temperate lands they are least numerous in winter and multiply spasmodically at other times in relation to the weather conditions and to the growth of higher plants (e.g. in deciduous woodlands). In arid or tropical regions rainfall seems to be the major factor determining their periodicity.
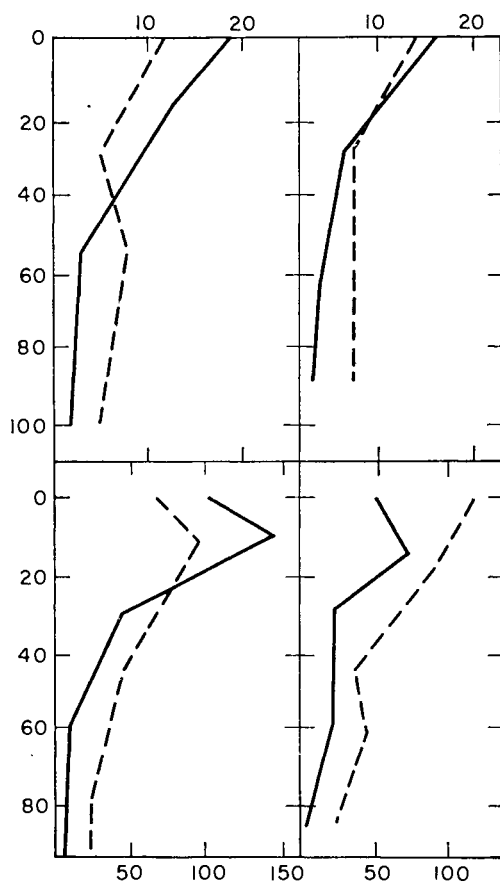
FIG. 1. Vertical distribution of algae in ploughed sod-podsol soils.
(a) 19 November, 1950; (b) 28 May, 1952; (c) 10 July, 1952; (d) 11 August, 1953.
————, cells; — — — —, species/g soil. Vertical axis, depth (cm). Horizontal axes, upper number of species $\times 10^{-3}$; lower, number of cells. Redrawn from Figs 5 to 8 of Shtina, 1959b.

II. EFFECTS OF PHYSICAL ENVIRONMENT

Soil algae and associated moss protonemata form the only microbial soil community dependent on light for its development. It is true that there is evidence for some growth within the soil but, as will be seen, this is only of limited extent. They are therefore exposed to the severe and often rapid changes in the physical conditions at the air-soil interface. It is, however, difficult to separate the effects of moisture, light and temperature on them in nature, though most of them are so cosmopolitan that their powers of resistance to adverse physical conditions must be considerable.

A. MOISTURE

In air-dried soil, live algae have been found after many years (Bristol, 1919; Becquerel, 1942; Lipman, 1941; cf. also Petersen, 1935). Nevertheless they rarely produce large populations except on damp soil (Stokes, 1940a; Brendemühl, 1949, *re* diatoms). This may be true even of arid areas where they depend on short, wet periods. However, waterlogging has been found to be unfavourable (Tchan and Whitehouse, 1953), perhaps because the experiments did not last long enough. If the soil does not become anaerobic, prolonged saturation permits new communities to appear. These, in my experience, are either typical of ephemeral aquatic habitats or transitional between those of soil and water. In some semi-deserts, such as the takȳrs of Russia (Bolȳshev and Evdokimova, 1944; Bolȳshev, 1952; Gollerbakh, Novichkova and Sdobnikova, 1956; Sdobnikova, 1958), there is an alternation of freezing conditions in winter, while in spring the thaw and the flood water from the mountains produce semi-aquatic or, in hollows and beds of streams, truly aquatic conditions. Finally, in summer it is extremely hot and dry. During spring the waterlogged soil is inhabited by vast growths of Cyanophyta, the dominant forms being species common to soil and water. In addition many other soil algae, especially Chlorophyta, are present.

Cells may die when dried in air but remain alive when immersed in soil which contains very little water and, superficially, appears to be dry (Petit, 1877; Bristol Roach, 1927a; Petersen, 1935; Evans, 1958, 1959). Diatoms as a whole seem to be the least resistant, but the data are somewhat contradictory. *Nitzschia palea* (Kütz.) W.Sm. grown in liquid culture died when dried in air (Denffer, 1949) but remained alive in soil which contained little water or was dried in air for 70 to 98 years (Bristol, 1919; Becquerel, 1942). It may be that different forms were investigated, but there is also no doubt that the conditions prevailing before drying and the rate at which this takes place affect the viability of cells (Petit, 1877; Lange, 1953; Füchtbauer, 1957a, b). One of the reasons for the prevalence of Cyanophyta in arid areas is their ability to withstand very wet and very dry conditions (e.g. Fay and Fogg, 1962) and rapid changes from the one to the other. In dry periods they often exist as mats or crusts and when heavy rain or floods come these rapidly imbibe water, expand and are not easily displaced.

B. TEMPERATURE

The effects of fluctuations in temperature, like those in moisture, depend partly on the previous history of the cells and the rapidity with which it rises (e.g. Glade, 1914) or falls (e.g. Höfler, 1951). Some algae can live at temperatures equal to or beyond any to which they will be exposed in nature (Glade, 1914; Kärcher, 1931; Becquerel, 1936; Booth, 1946; Kingsbury, 1956; Trainor, 1962; Trainor and McLean, 1964). Drought may be the cause of death at high or low temperatures for the rate of freezing is important in relation to loss of water (Höfler, 1951). Despite the very low temperatures,

algae are common or abundant in alpine, arctic and antarctic areas (Koshe-leva and Novichkova, 1958; Dorogostaïskaya, 1959; Roïzin, 1960; Dr E. Flint, Sir V. Fuchs and Dr W. H. Holdgate, personal communications). However, in more temperate lands it seems that cold is probably one of the main reasons for the reduction in algal numbers in winter (Lund, 1947; Shtina, 1959b). It does not follow that the cells die; it could be that the rate of loss (e.g. from rainfall) becomes relatively greater because the rate of growth of the algae has decreased. The abundance of algae in hot climates is referred to several times in this chapter. While about 50° C is near or above the maxi-mum temperature of the surface of the soil in temperate regions (Geiger, 1950), 70° C or higher is known for arid or tropical areas; for example 75° C on takȳrs with algae (Sdobnikova, 1958). The highest recorded temperature on takȳrs is above 87°C (Kovda, Bazilevich and Rodin, 1956). Under such con-ditions the moisture content of the soil may fall to 1 to 2% and in winter the ground is frozen, the lowest temperature recorded for the surface soil being $-11.5°$C (Kovda et al., 1956). Despite such a severe climate not only are Cyanophyta very abundant over a great area but about 150 spp. of algae have been recorded (Gollerbakh et al., 1956). Similar data, apart from low winter temperatures, are recorded for Death Valley, California, U.S.A., where the air temperature reaches 57°C and that of the ground 88°C. Annual rainfall averages about 4 cm and the evaporation power of the environment is equal to a surface loss of about 370 cm (Durrell, 1962).

III. EFFECTS OF CHEMICAL ENVIRONMENT

A. pH AND IONIC BALANCE

More has been written about the range of pH tolerated or favoured by soil algae than any other chemical factor (Shelhorn, 1936; Gollerbakh, 1936; John, 1942; Lund, 1945–46, 1947; Zauer, 1956; Shtina, 1959b). The ease with which pH can be measured, but not always in such a manner that the true soil value is found, has led perhaps to over-emphasis on this factor. Most species can grow on soil which is neither very acid nor very alkaline (e.g. pH 5·5 to 8·5). The widest diversities of species are found on neutral to moderately alkaline soils. Such soils are usually productive but large crops, composed of a few species, may be found elsewhere. On highly acid soil Chlorophyta often predominate and on the more alkaline ones, including those which are saline or arid, Cyanophyta are usually prominent. A few species seem to be calciphobes, notably Euglena mutabilis Schmitz, which is common on peat and may flourish at pH 1 to 3 (Lackey, 1938; Prát, 1955; Fott, 1956; U.K. National Coal Board, in litt.).

pH is so bound up with other factors, notably the calcium carbonate con-tent of the soil, that it is difficult to know how far it determines the flora. An example of the effect of the ratio of mono- to divalent cations is provided by Monodus subterraneus Boye Pet., which grows well up to pH 8 to 9, provided this ratio is high (Miller and Fogg, 1957). Algae must often be exposed to

rapid changes of salinity in relation to the drying and wetting of the surface of the soil. Many are also found on saline soils and in salt marshes. The addition of solid inorganic fertilizers produces rapid growth, especially of green algae, and several species are resistant to or are stimulated by the addition of seawater or sodium chloride (e.g. Gistl, 1932; Pringsheim and Pringsheim, 1956; Allen, 1956; Rieth, 1962a; Fay and Fogg, 1962).

B. INORGANIC NUTRIENTS

Most of the information about the nutrition of soil algae concerns compounds of carbon, nitrogen and phosphorus. Probably much information is concealed in the vast literature on the physiology of *Chlorella*. Unfortunately the natural habitats of most *Chlorellae* in culture are not known.

It might seem that silicon would never be lacking for the amounts are high compared to those of freshwaters in which shortages of this element have been demonstrated. Further, the algae often live apposed to more or less siliceous particles, and so where the concentration may be expected to be highest and new supplies most rapidly produced. However, the decomposition of siliceous minerals by diatoms (see Hutchinson, 1957) may be a reflection of the adjustment of the equilibrium between mineral silicates, silica in solution and diatom silica; rather than the solution of mineral silica by the excretion of special compounds. The weak silicification of some soil diatoms may be inherent or related to other factors, for they are often accompanied by heavily silicified forms (Hustedt, 1942). I have never found a population solely composed of weakly silicified species. Nevertheless the detailed study of *Navicula pelliculosa* (Bréb.) Hilse shows that silicon can affect the formation of the wall and the rate of growth, while its uptake may be affected by other substances (Lewin, 1954, 1955a, b, 1957). Therefore the amount of silicon in the soil solution may be important for diatoms as it is for rice and other grasses.

The importance of calcium is clear from the discussion of pH. Its effect is more evident in the quality of the flora than in its richness, because calcareous soils are so often relatively rich in nitrates and phosphates (e.g. Lund, 1945–46, 1947). There is little information about potassium. When grasses, clover and Cyanophyta were grown in pots, the last flourished in all those devoid of the Angiosperms. When grown with the Angiosperms, Cyanophyta only flourished when fertilizers were added. A mixture of phosphorus and potassium was specially effective and ammonium nitrate ineffective. Addition of potassium has less effect than that of phosphorus (Knapp and Lieth, 1952; Schwabe, 1963).

The effects of phosphorus and nitrogen are often considered together. Lund (1945–46, 1947) found that soils relatively rich in phosphates and nitrates were also the richest in algae. Shtina (1959b) added phosphate to soil but did not find it had marked effects on the diatoms. She says, however, that it may be that her experimental plots contained sufficient phosphorus before fertilization. Green algae may abound on soil poor in nitrates and phosphates, but

they are also stimulated by inorganic nitrogeneous fertilizers. Some of them grow well on acid soil but one reason why Knapp and Lieth (1952) found NH_4NO_3 so ineffective in their experiments with Cyanophyta may be increased acidity of the soil, ammonia being preferentially utilized (cf. Syrett, 1954). Phosphate added to rice fields increases the crop of Cyanophyta (Singh, 1961). It should be said here that the common assumption that the algae of rice fields are soil algae, that is terrestrial algae, is not necessarily true. Some are wholly aquatic, others are common to soil and water. The development of the soil community will be affected by the degree of flooding of the fields. This can vary in relation to local practice or the developmental stage of the crop.

A few algae seem to be nitrophilous (Petersen, 1928; Knebel, 1935; Barkman, 1958). The best known example is *Prasiola crispa* Menegh. Enormous growths are found where birds abound, for example in Penguin rookeries. Samples from the soil around Puffin (*Fratercula arctica*) burrows on the Farne Islands, England, when dried, contained 8·9% of nitrogen, a very high figure for a Green alga in nature. It is not known whether both inorganic and organic nitrogen are used, but some Cyanophyta can use the latter and hydrolyse proteins (Allen, 1952). *Porphyridium purpureum* (Bory) Drew and Ross (*P. cruentum* (S. F. Gray) Hansg. and including *P. marinum* Kylin) also seems to be nitrophilous though a high phosphorus content in the soil may also be important (Rieth, 1961, 1962a, b; Rieth and Sagromsky, 1964).

Several Cyanophyta which are common on soil can fix nitrogen. The abundance and often dominance of Blue-green algae on tropical and subtropical soils (Esmarch, 1911; Duvigneaud and Symoens, 1949; Mitra, 1951; Singh, 1961; Durrell, 1964; personal observations on East African soils collected by Drs J. F. and I. Talling) which are so often deficient in nitrogen, may be related in part to this ability. There is abundant evidence that they do fix nitrogen under natural conditions, especially in arid soils (Fletcher and Martin, 1948; Shields, Mitchell and Drouet, 1957; Cameron, 1960; Cameron and Fuller, 1960; Singh, 1961; Shields and Durrell, 1964; Shtina, 1965; Tret'yakova, 1965). The fixation of nitrogen by Cyanophyta in rice fields has received much attention (see Singh, 1961, for a review up to 1959 and for original data). Other temporarily inundated areas may also benefit from the growth of Blue-green algae (e.g. Saubert and Grobbelaar, 1962). Both Japanese and Indian agriculturalists add fertilizers (notably phosphates, sometimes with molybdenum) and, if necessary, also lime to raise the pH. It is considered that under these conditions Blue-green algae are an effective substitute for nitrogenous fertilizers such as ammonium sulphate and, if the soil is poor, far superior to them (Subrahmanyan, Relwani and Manna, 1964a, b). Watanabe (1960) has grown mass cultures of *Tolypothrix* and then inoculated rice-fields with the alga (Watanabe *et al.*, 1959). The alga exerted a marked and long-lasting effect on the growth of the rice (Watanabe, Nishigaki and Konishi, 1951). The influence of the algae is not confined to the wetter periods of cultivation. Their cellular nitrogen is soon released after death by bacterial action, ammonia being the chief end product (Fedorov,

1952; Watanabe and Kiyohara, 1960). However, Sulaiman (1944) says that there is a loss of nitrogen when dried algae from a rice field decompose *in situ*. On the other hand part of the nitrogen they fix will be available to the rice while they are alive in the form of extracellular products (Fogg, 1960). After two months, in experiments with rice in a medium lacking added nitrogen, plants in containers with a nitrogen-fixing *Anabaena* had 10 times the dry weight and contained 20 times as much nitrogen as those to which no alga had been added (Allen, 1956). Cameron and Fuller (1960) found that from none to over half of the nitrogen fixed by species from soil was present in culture media. Algae are not always beneficial to rice, for young plants may be harmed if algal mats and scums are too abundant (Bunt, 1961). Rice plants may increase the growth of the algae, and a similar effect is obtained in their absence by aerating with carbon dioxide (De and Sulaiman, 1950).

Although these investigations mainly cover algae growing on waterlogged or underwater soils, the results may well indicate what happens in ordinary soil. Singh (1961) finds that considerable fixation occurs in India in fields of sugarcane and maize, on fallow land and in grassland. However, doubt has also been expressed about the contribution made by Cyanophyta to the nitrogen economy of soil (Stokes, 1940b). Cyanophyta are only abundant on neutral or alkaline temperate soils and these are usually richer in nitrates than acid ones. If ammonia or nitrates are present, fixation of nitrogen may be depressed (De, 1939; Fogg, 1960). In the laboratory, Blue-green algae commonly become more predominant the longer the soil is kept moist and free of plant-cover (Drewes, 1928; John, 1942; Lund, 1947). The reason for this is unknown. Fogg (1960, in discussion, cf. Lund, 1947) suggests that the available nitrogen in the algal mats may be exhausted and that free nitrogen will diffuse in more rapidly than combined nitrogen so that fixation is occurring in these algal strata. Drewes (1928) found that Cyanophyta become dominant early in an enriched soil if phosphorus but not nitrogen has been added to it but much later if salts of both elements are supplied originally. Even in some semi-arid regions where Cyanophyta cover considerable areas, the amount of nitrogen fixed may be so small that it cannot be detected on a yearly basis using the Kjeldahl technique for its estimation (Tchan and Beadle, 1955). However, the algae concerned may be different from those forming crusts in the arid regions referred to earlier. The algae are found mainly beneath translucent pebbles and stones. These "Fensterpflanzen" (Vogel, 1955) have been observed in Australia, Egypt, Sudan, South Africa and the U.S.A. (Williams, 1943; Tchan and Beadle, 1955; Vogel, 1955; Durrell, 1962). Samples collected for me from East Africa by Dr J. F. Talling were dominated by Chroococcaclae, a family not known to contain any nitrogen-fixing species. The algae grow on the parts of the stones at or below the surface of the soil and will be protected from extremes of light and temperature. It may be that conservation of moisture is the main advantage of life under translucent stones. Moisture is often only available as dew which will condense on the stones during the night.

It is not known whether deficiencies of trace elements known to affect

Angiosperms in nature also influence the growth of algae. The range of essential elements for soil algae may well be the same or very similar to that needed by algae elsewhere judging from Eyster's (1958, 1959, 1964) work on *Nostoc muscorum* Ag. ex Born. et Flah. and Wiessner's (1962) review. Molybdenum is concerned in nitrogen fixation (Fogg, 1960, in discussion; Singh, 1961) and has been added to soil from rice-fields containing algae. In the light, with the addition of phosphorus, more nitrogen was fixed than with phosphorus alone. In the dark algae were absent and nitrogen fixation was insignificant, indeed in two cases nitrogen was lost from the soil (De and Mandal, 1956).

C. ORGANIC MATTER—HETEROTROPHY

Many soil algae can grow in the dark if suitable organic compounds are present, notably glucose, which, however, will be rapidly utilized by most soil microbes. Some species can only grow in the light (obligate phototrophs, Fogg, 1953; Parker, Bold and Deason, 1960; Parker, 1961). It is not surprising that the pioneer studies of Bristol Roach (1926, 1927a, b, c, 1928) led to the view that the frequent occurrence of algae within the soil probably was the result of the active multiplication of cells within it. Later workers (Petersen, 1935; De and Sulaiman, 1950; Stokes, 1940a; Tchan and Whitehouse, 1953) came to the opposite conclusion, for they could not detect any significant increase in algal numbers in soil kept in the dark even when glucose was added. It is significant that in the desert areas referred to earlier, the algal communities are only found under translucent pebbles. Nevertheless recent experiments (Parker and Bold, 1961; Parker, 1961) suggest that facultative heterotrophy can be of ecological importance. If suitable bacteria or actinomycetes are present some of the algae will grow in the dark, though, as will be seen, the interrelationships are complex and vary markedly from alga to alga. The largest increase found in soil and water cultures was sixteenfold in 14 months. This is equivalent to only 4 cell divisions or the production of one or two autosporangia in over a year. As other algae would not grow in the dark, it is not surprising that workers have failed to detect any increases in the populations as a whole. The rate of growth of many such small algae in the light can be equivalent to about one cell division per day, so that an increase equal to that in about 60 weeks in the dark could be produced in less than one week in the light. Facultative heterotrophy, therefore, seems to be of biological value in maintaining populations buried in the soil but is of little importance in production as a whole. As Schwabe (1963) says, there is indirect support for this view in that macroscopic strata of Blue-green algae are only found on the surface. This is equally true of discolorations by Green algae and Xanthophyceae. Heterotrophy may explain the records of comparatively large populations in the rhizosphere (Shtina, 1954, 1961; Hadfield, 1960; Gonsalves and Yalavigi, 1960), though it remains to be seen whether algae are relatively easily washed into the soil down the passages made by roots and to what extent such populations differ from those at a distance from roots (cf. Troïtskaya, 1961) and are composed of facultative heterotrophs.

Fresh dung seems to be inimical (Stokes, 1940a; Shtina, 1963; personal

observations) probably because of the vast growth of other micro-organisms and the exclusion of light. Later, as in sewage lagoons, very large populations may arise (cf. Shtina, 1959b, 1963, and personal observations).

IV. INTERRELATIONS WITH OTHER ORGANISMS

A. MICRO-ORGANISMS

The interrelations between algae and other soil organisms are little known. Grazing has scarcely been studied (Nielsen, 1949; Bunt, 1954; Schwabe, 1960a; Kühnelt, 1961) and nothing is recorded about parasites. The discussion on heterotrophy has shown that bacteria and actinomycetes may permit algae to grow in the dark, but these interrelationships are affected by the type of soil. There is still controversy over the effect of algae on *Azotobacter* and the relative importance of this bacterial genus and Cyanophyta in the fixation of nitrogen in many soils. Early workers believed that soil algae, even if they did not fix nitrogen themselves, stimulated the growth of *Azotobacter*. The discovery that many Cyanophyta fix nitrogen, that marked increases in the nitrogen in algal and lichen associations arise in the absence of *Azotobacter*, and that live or dead growths of other algae do not seem to assist this or other nitrogen-fixing bacteria, caused a change of view (e.g. Drewes, 1928; Clark, 1936; De, 1939; Stokes, 1940a; Martin, 1940; Sulaiman, 1944; Russell, 1950; Cameron and Fuller, 1960). However, some modern authors find that algae do stimulate *Azotobacter* or that algae and bacteria together may fix more nitrogen than either do alone (Szolnoki, 1951; Fedorov, 1952; Shtina, 1959b, 1961; Bjälfve, 1962; Shtina and Yung, 1963, Fedorov (1952) points out that if moist, pure sand is exposed to the light the nitrogen content increases, while in the dark it does not, and that this increase is accompanied by a visible greening of the surface. Parker and Turner (1961) and Bjälfve (1962) produced good experimental evidence against an interaction between some algae and *Azotobacter*. The nitrogen fixed in the latter's mixed culture was almost exactly the sum of the increases when *Nostoc calcicola* Bréb. and *Azotobacter* were grown separately. However, in dual cultures with some other bacteria more nitrogen was fixed than when *Nostoc* grew alone. In the case of *Rhizobium* spp. and *Nostoc* the fixation might be expected to be by the latter, but a curious feature of the cultures was the appearance of bacteroid forms similar to those in nitrogen-fixing nodules of Leguminosae. In earlier work Clark (1936) did not find any fixation of nitrogen in cultures containing the Green alga *Chlorella* and *Rhizobium*. A number of interactions between algae and fungi or bacteria have been described from observations on natural populations and laboratory experiments. Fletcher and Martin (1948) found that if crusts from the Arizona desert were kept moist for more than a week, the algae degenerated and fungi took their place. Cribb's (1955) and Litvinov's (1956) descriptions of pale spots or rings in crusts of Blue-green algae are similar, though they were unaware of each other's work. The fungi concerned are Ascomycetes and an imperfect species, *Stemphylium algophagum* Litv. Other species of

Stemphylium are known to be stages of an Ascomycete (Ainsworth, 1961). The algae grow rapidly when rain follows drought. The later appearance of the fungus may be related to the reduced vigour of the alga after it has utilized nutrients in its vicinity, because Parker and Bold (1961), in different circumstances, found that the destruction of a *Phormidium* by a Basidiomycete in mixed culture could be prevented by enriching the medium with certain
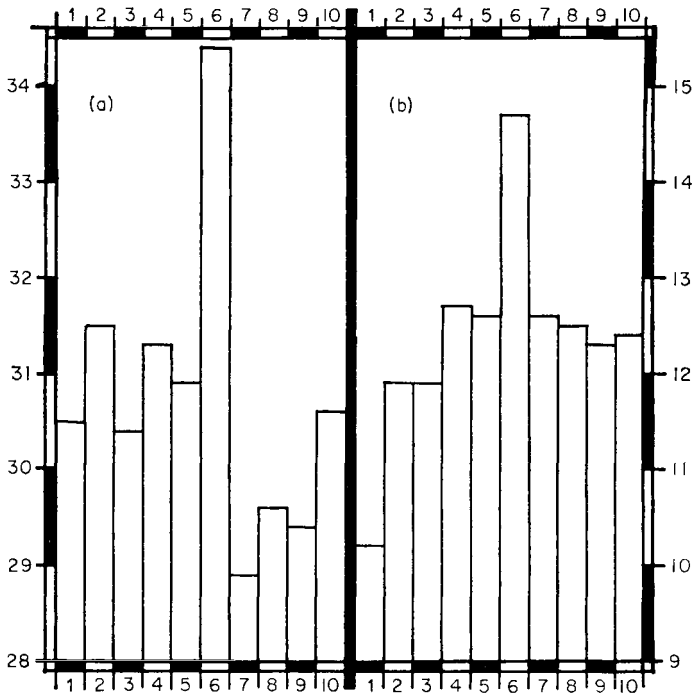

FIG. 2. Influence of *Azotobacter* and algae on the growth of oats.

Left-hand columns (a) weight of plants; right-hand columns (b) weight of grain. Each result the mean of four pot experiments. Horizontal axis; 1, control soil; 2, *Azotobacter* added to the soil and 3, to the oat seeds; 4 to 10, additions to soil: 4, *Azotobacter* on peat enriched with algae; 5, *Azotobacter* and Cyanophyta; 6, *Azotobacter* and Chlorophyta (mainly *Chlorella terricola* Gollerb.); 7, *Azotobacter* and filtrate from culture of Cyanophyta; 8, *Azotobacter* and filtrate from culture of Chlorophyta; 9, Cyanophyta; 10, Chlorophyta. Vertical axes, weight (g); right hand, plants; left hand, grain. (Based on Table 4 of Shtina and Yung, 1963.)

nitrogen compounds. Lack of available nitrogen by itself was not the cause of the death of the alga. The mechanisms involved in these interrelationships are not understood. A bacterium increased the growth of a coccoid Green Alga because of its ability to decompose organic nitrogen compounds (Parker and Bold, 1961). From 143 dual cultures, all involving at least one alga, a variety of results were obtained ranging from neither partner affecting the

other to each partner inhibiting the other. The majority of the heterotrophic organisms, Protozoa excluded, stimulated the algal partner (Parker and Turner, 1961). In some cases the growth of a fungus may depend on the presence of sufficient algal cells in its vicinity. For example, several soil fungi needing thiamin or its components could obtain them in a culture medium which did not contain them originally. Such a mixture of an alga and a fungus generally grew together without either inhibiting the other. In a few cases the alga was killed sooner or later, apparently by the exclusion of light when the fungus grew over it (Gaümann and Jaag, 1950).

B. HIGHER PLANTS

Inhibition is well known, but it is difficult to discover its ecological importance in nature. The same is often true of stimulation of one organism by another. In experiments with Angiosperms and Cyanophyta, the effect of the former on the latter is ascribed to inhibition (Knapp and Lieth, 1952) but the data are not very satisfactory. Piercy (1917) found that *Chlorohormidium flaccidum* (A. Br.) Fott only grew extensively in grassland in wet periods after drought had killed the grass and before a new sward was formed. Apart from those discussed, there are several other accounts of algae inhibiting or stimulating one another, Angiosperms, or other micro-organisms (Drewes, 1928; Flint, 1947; Bolyshev, 1952; Harder and Oppermann, 1953; Wolters, 1960; Jacob, 1954a, b, 1961). The germination of seeds may be unaffected or stimulated or inhibited by algae (Shtina, 1954, 1956a; Troïtskaya 1961; Novichkova, 1955). Shtina (1954, 1956a, 1959b, 1961) finds no evidence that roots of Angiosperms are inhibited by soil algae, but algal extracts may stimulate their development. The roots of some plants, but not those of conifers, may stimulate algal growth. She also found that algal extracts retarded the growth of some phytopathogenic fungi. Engle and McMurtrey (1940) found that algae protected tobacco roots, but it is not clear that they would do so in nature, when they would have no illumination. Enhanced growth of algae in the rhizosphere has been observed (Katznelson, 1946; Shtina, 1959b; Hadfield, 1960; Gonsalves and Yalavigi, 1960; Cullimore and Woodbine, 1963) but Katznelson (1961) and Troïtskaya (1961) could not detect any such effect. More data are needed, including information about the surface flora and soil treatment, before any general conclusions can be drawn from these divergent results.

V. EFFECTS ON SOIL

The data concerning rice-fields, cited previously, show that dead or live algae may act as fertilizers. In arid zones, algae may be important sources of organic matter (e.g. humus, Ponomareva, 1956; concerning nitrogen, see p. 136 and Shields and Durrell, 1964). It remains to be shown that in non-arid zones they are equally important. The abundance of algae on soils which are also fertile in relation to other plants has lead to their use for bio-assay

(Tchan, 1959; Tchan *et al.*, 1961). They may be considered more suitable for this purpose than the heterotrophs used because they are photosynthetic plants. Green algae, moreover, are in general similar in physiology and bio-chemistry to higher plants—indeed some taxonomists would include all "green" plants in one phylum. Other soil algae, notably diatoms and Cyanophyta, differ so markedly from Chlorophyta and in all groups there is such ecological and physiological diversity that a variety of techniques for bio-assay might be elaborated.

In man-made "deserts" or "dust bowls" algal crusts may bind soil particles together (e.g. Schwabe, 1960a, b; Durrell and Shields, 1961; Bond and Harris, 1964) and so prevent erosion and permit re-colonization by Angiosperms (Booth, 1941). There is, however, evidence for an alternative view, namely that algae are of little value in soil conservation, simply occupying spaces between or around the sparse vegetation. The crusts in the Arizona desert are said to interfere with infiltration of water into the soil (Fuller, Cameron and Raica, 1960) or to improve infiltration (Fletcher and Martin, 1948). They interfere with infiltration on takȳrs but also reduce the rate of water loss from the soil below them (Gollerbakh *et al.*, 1956). In Arizona, crust forma-tion reduces soil erosion except in storms, when the crust delays the penetra-tion of water and so increases erosion (Cameron, 1964). The classic story of the role of algae in the re-colonization of Krakatoa (Treub, 1888) is also disputed (Backer, 1929). Similarly the predominance of soil algae on rocks and thin soils in high-mountain arctic "deserts" (Roïzin, 1960) and their ability to "rot" rock does not necessarily mean that they are as effective in the break-down of rock as are frost, sunshine, wind and rain.

The study of soil algae lags behind that of many other micro-organisms. The most extensive investigations have been carried out in Russia and, in relation to waterlogged or underwater soils of rice fields, in India and Japan. We need, among other things, methods for determining productivity, detailed observations on seasonal periodicity and more laboratory experiments which, so far as is possible, are so devised that the results are likely to be relevant to practical problems.

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